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COMPARATIVE SPECIATION IN TWO BUTTERFLY FAMILIES, PIERIDAE AND NYMPHALIDAE

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IT IS NOWADAYS GENERALLY ACCEPTED that the main factors influencing evolution are mutation, recombination, selection, chance, and isolation. Naturally these five factors do not play the same rôle in all groups of animals and plants. Thus, for instance, the evolution of polyploid forms is of much greater importance in plants than in animals. Similarly the selective forces affecting the evolution of protozoans and mammals must be very different. The branch of biology dealing with such problems we may call comparative evolution in analogy with comparative anatomy.

Comparative speciation, with which this paper is concerned, is a part of this science. An important method is here to compare the differences existing between the closest related species of different groups. Such differences must be the result of the evolution having taken place since the time of the common ancestral form. It is possible that the differences evolved are an integrating part of the mechanism isolating the two species. In other cases the differences may be the result of adaptations to different environmental conditions or be just a matter of chance.

The two groups discussed here are the two butterfly families *Pieridae* and *Nymphalidae*. All sympatric closely related European species of these two families are compared. To these species the two North American sibling species *Colias eurytheme* and *C. philodice* have been added as they are especially well known predominantly from the investigations by Hovanitz (1943, 1948, 1949 a, b).

Fam. *Pieridae*.

1. *Pieris napi* L. — *P. bryoniae* Ochs.

These two forms do not behave as different species in all areas where they meet. They do however in some areas which justifies a discussion of their differences.

Male patterns rather similar.

Female patterns more extended in *bryoniae* than in *napi*. Male wing color similar, female wing color white in *napi*, yellow in *bryoniae*.

Genitalia similar (Drosihn 1933).

Foodplants: *napi*: various cruciferous plants.

bryoniae: *Biscutella laevigata*.

2. *Pieris napi* L. — *P. ergane* Hbn.

The patterns of *ergane* are closer to those of *P. rapae* than to those of *napi*. The color of the females is sometimes yellow in *ergane*, less often in *napi*. The genitalia are similar (Drosihn 1933) as well as the scent of the males (Lorkovic, personal communication).

Foodplants: *napi*: various cruciferous plants.

ergane: various cruciferous plants (Forster and Wohlfahrt 1955, Verity 1947), *Aethionema saxatile* in the French Alps and Pyrenees (Descimon 1964, 1966). The very local occurrence of this species makes a wide variety of foodplants rather unlikely.

3. *P. rapae* L. — *P. manni* Mayer.

The patterns of the two species are rather similar, the background color of the females less yellow in *manni* than in *rapae*. Genitalia similar.

Foodplants: *rapae*: various cruciferous plants.

manni: *Diplotaxis tenuifolia* (Italy), *D. eruroides*, *Lepidium graminifolium*, *Iberis* spp., not on cultivated cruciferous plants (Verity 1947).

4. *Colias hecla* Lef. — *C. nastes* Bdv.

The patterns are markedly different in the males, less so in the females. The color is in both sexes orange in *hecla* and yellow in *nastes*.

Genitalia very similar. The number of teeth of the aedeagus on the average slightly higher in *hecla*. Only one specimen of 41 + 34 outside the range of variation of the other (Peterson 1963 b).

Foodplants: *hecla*: *Hedysarum americanum*, *Astragalus alpinus*.

nastes: *Astragalus deflexus* and *alpinus*.

5. *C. hyale* L. — *C. australis* Ver.

Slight differences are present in the patterns. The yellow color in *australis* is more "beautiful", in *hyale* more greenish and "dirty" (Reissinger 1960).

Genitalia slightly different (Warren 1951, Beuret 1951, Bretschneider 1959, Schadewald 1959). Berger and Fontaine (1947), Reissinger (1960), and Petersen (1963 b) found no differences.

Foodplants: *hyale*: various leguminose plants.

australis: *Hippocrepis comosa*.

Male scent: *hyale*: strong aromatic scent (Berger and Fontaine 1947), rather peppery (Riley 1961).

australis: absent or almost absent (Berger and Fontaine 1947), sweetish, honeylike (Riley 1961).

6. *C. myrmidone* Esp. — *C. erate* Esp.

The patterns are markedly different in the males less so in the females. The color is orange in *myrmidone*, usually yellow in *erate*.

Genitalia very similar (Petersen 1963 b).

Foodplants: *myrmidone*: *Cytisus* spp.

erate: unknown.

7. *C. eurytheme* Bdv. — *C. philodice* Gdt.

As in two of the previous *Colias* species the pattern differences are greater in the males than in the females. Color is in *eurytheme* orange, in *philodice* yellow.

Genitalia very similar (Petersen 1963 b).

Foodplants: *eurytheme*: *Medicago*.

philodice: *Trifolium*.

Male scent of *eurytheme* like sweet heliotrope.

8. *C. aurorina* H. Sch. — *C. sagartia* Led.

Pattern differences about the same as in previous species. The color is in *aurorina* orange, in *sagartia* bluish green.

Genitalia very similar (Petersen 1963 b).

Foodplants unknown.

Only *C. aurorina* occurs in Europe. *C. sagartia* lives in S. W. Asia.

9. *Gonepteryx rhamni* L. — *G. cleopatra* L.

There are hardly any patterns on the wings of the two species. The forewings of *cleopatra* males are orange except along the borders, and the yellow color is more saturated. The females of *cleopatra* have yellow borders on the wings.

Genitalia: uncus much smaller in *cleopatra*, otherwise rather similar (Verity 1947).

Foodplants: *rhamni*: *Rhamnus* spp., *Vaccinium*, *Rosa*, *Prunus spinosa*.

cleopatra: mainly on other *Rhamnus* spp. than

rhamni (Verity 1947).

Male scent: *rhamni*: absent.

cleopatra: rich and powerful, freesia (strong) (Ford 1945).

10. *Anthocaris cardamines* L. — *A. damone* Boisd. and *A. euphenoides* Stgr.

The two latter species are allopatric but not contiguous. The areas of distribution come fairly close together in Italy (cf. Verity 1947). Their great similarity suggests conspecificity. At least, they may both have arisen jointly from the *cardamines* stock and therefore cannot be treated here as two independent cases.

The differences in pattern between *cardamines* and *damone* are slight compared with the geographical variations within the species. The ground colors of the males (yellow in *damone* and white in *cardamines*) are strikingly different. The differences between the females are slight or none.

Genitalia differences are only of a quantitative nature (Verity 1947).

Foodplants. *cardamines*: various cruciferous plants. *Reseda*.
damone: *Isatis tinctoria* and *canescens*.
euphenoides: *Biscutella* spp.

Fam. Nymphalidae.

Mellicta Billb.

Higgins (1955) divides this genus into twelve species, seven of which occur in Europe. Three of these species, *aurelia* Nick. *deione* Geyer, and *asteria* Freyer together with the subsp. *athalia celadussa* Fruhst. do not redevelop subuncal processes below the tegumen. Verity (1950) is of the opinion that *M. deione* and *athalia celadussa* are most similar and he connects on the other hand *M. aurelia* with *M. asteria*. It may very well be that one subspecies (A_1) of one species is closest to one of the other species (B), while another subspecies (A_2) is closer to a third species (C). *M. athalia* with its marked intraspecific variation in the genitalia may very well be a species of type A. This, however, is of lesser significance in the present investigation as the differences in the genitalia between the forms mentioned are in all cases small but well distinct, colors similar, patterns similar or rather similar.

11. *M. deione* — *M. athalia celadussa*

Colors and patterns similar but variable.

Genitalia: small but distinct differences (Verity 1950).

Foodplants. *deione*: *Linaria* spp., *Antirrhinum* spp.

athalia celadussa: *Melampyrum*, *Plantago*.

12. *M. aurelia* — *M. asteria*.

Colors and patterns similar. *M. asteria* much smaller.

Genitalia. small but distinct differences (Verity 1950 p. 196).

Foodplants: *aurelia*: *Melampyrum*, *Veronica*, *Digitalis*, *Chrysanthemum*, *Plantago*.

asteria: unknown.

13. *Euphydryas cynthia* Schiff. — *E. intermedia* Mén.

Color similar in the females, different in the males. Patterns more different in the males than in the females.

Genitalia: slightly different (Higgins 1950).

Foodplants. *cynthia*: *Alchemilla*, *Plantago alpina* and *lanceolata*, *Viola*, *Vaccinium myrtillus*, *Pedicularis*.

intermedia: *Fraxinus*, *Populus*, *Salix*, *Alnus*, *Viburnum*, *Melampyrum*, *Veronica*, *Scabiosa*, *Plantago*, *Viola*, *Prunus*, *Lonicera* (Verity 1950).

14. *Fabriciana adippe* Rott. — *F. niobe* L.

Color and patterns rather similar on the upper side; on the under side the colors are rather different.

Genitalia: various parts shorter and thicker in *niobe* (Verity 1950).

Foodplants: *adippe*: *Viola* spp.

niobe: *Viola* spp., *Plantago* spp.

15. *Brenthis ino* Rott. — *B. daphne* Schiff.

Patterns are slightly different in both sexes on both sides of the wings. Colors are similar.

Genitalia: Verity (1950 p. 259) states that the differences found by Warren (1944) and dos Passos and Grey (1945) are individual variations present in both species.

Foodplants: *ino*: *Sanguisorba*, *Spiraea*, *Rubus*.

daphne: *Rubus*, *Viola*.

16. *Boloria pales* Schiff. — *B. aetha* Hemming (*arsilache*) Esp.)

Colors are similar in both sexes, patterns slightly different.

Genitalia: I was not able to confirm the differences found by Warren (1944).

Foodplants: *pales*: *Viola* spp.

aetha: *Vaccinium oxycoccus*, *Polygonum* spp., *Viola* spp.

17. *Boloria frigga* Thnbg. — *B. improba* Btl.

B. improba is much darker and smaller than *frigga*. The patterns on the under side are rather similar.

Genitalia: Slight differences are present (Bruun and von Schantz 1949).

Foodplants: *frigga*: *Rubus chamaemorus* (Lingonblad 1946).
improba: probably *Salix herbacea* (Bruun and von Schantz 1949).

In tables 1 and 2 the differences between the species have been summarized and indicated by value symbols. It is not always easy to decide which symbol should be used but the tendency is quite obvious: the differences in patterns are of the same magnitude in both families while differences in color are more marked in the *Pieridae*. Specific differentiation without any or with very little change in the genitalia is the rule in the genera *Pieris* and *Colias*, but has probably also taken place in *Brenthis* and *Boloria*.

When the colors of the *Nymphalidae* are different the differences are usually restricted to the under side, except for intrusion of melanistic scales on the upper side as in *Boloria improba* as compared with *frigga*. In the *Pieridae* the color differences are most striking on the upper side and are due to the intrusion of white, yellow, and orange pterins. In the *Colias aurorina*-group blue pigments are also present. In the genus *Colias* both sexes are different in color, in *Pieris* only the females, and in *Gonepteryx* and *Anthocaris* mainly the males. In the genera *Pieris* and *Colias* where the interspecific variation in female color is greatest, the differentiation in the male genitalia is less pronounced.

There are several reasons why closely related pierid species should be more divergent in color than *Nymphalids*. Pterins of white, yellow, and orange color are chemically related. The yellow color of *P. bryoniae flavescens* turns white when the pupae are exposed to pure oxygen during their development. Species of other families do not change color after similar treatment (Deschka and Reichl 1964). A mutation changing the wing color may happen more often in butterflies having pterins in their wing scales than in other Lepidoptera.

The colors of butterflies have several functions: warning, concealment, sexual attraction and stimulation. In connection with isolation between species the sexual functions are of special interest. The colors of the females are known to attract the males though supraoptimal colors sometimes are present (Tinbergen et al. 1952, Petersen et al. 1952). Thus the yellow color

of *P. bryoniae* females is less attractive to their males than the white color (without ultraviolet) of *napi* females and males of both forms. Yellow color may have a higher selective value because yellow females are less likely to hybridize. The yellow color may also be part of a protective coloration.

The colors of the males have been supposed by Ford (1953, 1965) to have a sexually stimulating effect. As far as I know conclusive experiments are still lacking. The presence of strikingly different colors in so many sibling species supports Ford's hypothesis and makes experimental evidence even more desirable.

Differences in the foodplants of the larvae are very marked. In one case only, *P. napi* - *ergane* some authors mention "different cruciferous plants" for both species. *Aetionema saxatile* is at least in France the most important foodplant for *ergane*.

In nine of the seventeen pairs of table 1 one of the species has a very wide distribution compared with the other. These species have been underlined in the table. As *P. napi* is present in two pairs there are together eight species of this kind. These eight species are all adapted to a temperate climate, some of them also to colder and warmer climates. Their larvae live in seven cases on plants of more than one genus while six of the species with restricted distributions live on only one plant genus, usually on a single species. Ecologically they are adapted to an Arctic or alpine climate or to the climate of the Mediterranean area.

The wider ecological amplitude of the central species compared with the 'edge' species is in agreement with the ideas of Brown (1957). He points out that central species are more "potent" and therefore the source of higher categories. Contrary to this Mayr (1954) has stressed the importance of the edge populations, especially on islands. Such isolated populations can under unique environmental conditions form the real novelties of the animal world. It may be noted that the only novelty (not real novelty) among the species treated here belongs to the edge species: *Boloria improba*. Living at a higher altitude than any other Scandinavian butterfly and with a concealing coloration well adapted to the dark rocks and stones at this it may be potentially equivalent to the many small *Erebia* and *Mellicta* spp. etc. of the higher parts of the Alps. However, the evolution of a new (sub) genus under such extremes is rendered less

Species	Differences in				Larval foodplant
	pattern	color	genitalia		
family Pieridae	♂	♀	♂	♀	
1. <u>PIERIS NAPI</u> / <u>bryoniae</u> (a)	(+)	+	-	+	cruciferous plants / <u>Biscutella laevigata</u> cruciferous plants / cruciferous plants
2. <u>PIERIS NAPI</u> / <u>ergane</u> (m)	(+)	(+)	-	(+)	<u>Aethionema saxatile</u>
3. <u>P. RAPAE</u> / <u>manni</u> (m)	(+)	(+)	-	(+)	cruciferous plants / <u>Diplotaxis tenuifolia</u>
4. <u>Colias hecla</u> (a) / <u>C. nastes</u> (a)	+	(+)	+	+	<u>Hedysarum americanum</u> , <u>Astragalus alpinus</u> / <u>Astragalus deflexus</u> , <u>alpinus</u>
5. <u>C. HYALE</u> / <u>australis</u> (m)	(+)	(+)	(+)	(+)	leguminous plants / <u>Hippocrepis comosa</u>
6. <u>C. myrmidone</u> / <u>erate</u>	+	(+)	+	+	<u>Cytisus</u> spp. / unknown
7. <u>C. erytheme</u> / <u>philodice</u>	+	(+)	+	+	<u>Medicago</u> / <u>Trifolium</u>
8. <u>C. aurorina</u> / <u>sagartia</u>	+	(+)	+	+	unknown
9. <u>Goneperyx rhamnii</u> / <u>cleopatra</u> (m)		+	+	(+)	<u>Rhamnus</u> spp., <u>Vaccinium</u> , <u>Rosa</u> / <u>Rhamnus</u> spp.
10. <u>Anthocharis cardamines</u> / <u>damone</u> + <u>euphenoides</u> (m)	(+)	(+)	+	(+)	cruciferous plants / <u>Isatis tinctoria</u> + <u>Biscutella</u> spp.
family Nymphalidae					
11. <u>MELICTA ATHALIA celadussa</u> (+) / <u>deione</u> (m)	(+)	-	-	-	<u>Melampyrum</u> , <u>Plantago</u> / <u>Linaria Antirrhinum</u>
12. <u>M. aurelia</u> / <u>asteria</u> (a)	-	-	-	-	<u>Melampyrum</u> , <u>Plantago</u> , <u>Veronica Digitalis</u> , <u>Chrysanthemum</u> / unknown
13. <u>Euphydryas Cynthia</u> (a) / <u>intermedia</u> (a)	+	(+)	+	+	<u>Alichemilla</u> , <u>Plantago</u> , <u>Viola</u> , <u>Vaccinium</u> , <u>Pedicularis</u> / <u>Fraxinus</u> , <u>Populus</u> , <u>Salix</u> , <u>Plantago</u> , <u>Viola</u> , <u>Alnus</u> , <u>Viburnum</u> , etc.
14. <u>Fabriciana adippe</u> / <u>niobe</u>	(+)	(+)	+	+	<u>Viola</u> / <u>Viola</u> , <u>Plantago</u>
15. <u>BRENTIS INO</u> / <u>daphne</u> (m)	(+)	(+)	-	+?	<u>Sanguisorba</u> , <u>Spiraea</u> , <u>Rubus</u> , / <u>Rubus</u> , <u>Viola</u> ceae
16. <u>Boloria aethea</u> / <u>pales</u> (a)	(+)	(+)	-	-?	<u>Viola</u> , <u>Vaccinium ocyrococcus</u> , <u>Polygonum</u> , / <u>Viola</u>
17. <u>Boloria frigga</u> / <u>improba</u> (a)	+	+	(+)	(+)	<u>Rubus chamaemorus</u> / <u>Salix herbacea</u>

Table 1. Presence or absence of differences in some characters between sibling species of the families Pieridae and Nymphalidae. (+) = slight differences in color and pattern. Species in caps = widely distributed species. a = adapted to arctic or alpine climate; m = distribution mainly in the Mediterranean area.

probable on account of the hazardous conditions for survival during the long time required for such a process.

The more restricted ecological amplitude of the edge species may in some cases depend on competition from the central species. Sometimes, however, this is certainly not the explanation. *P. bryoniae* and *A. euphenoides*, two edge species, both live on *Biscutella*. This is the only plant genus of the family *Cruciferae* which is common at the altitude where the butterflies live. The close relationship larva — foodplant might from the beginning have been more or less a matter of coincidence following the adaptation to a certain climate and a plant family as source of food.

However, as soon as the relationships have become established they become closer. When today *P. bryoniae* lives on *Biscutella* on the southern side of the Alps it is able to compete with *P. napi* down below 300 m (Posavje, near Ljubljana, Yugoslavia). When both live on *Arabis halleri*, as on Monte Mottarone in the Italian Alps, the lower limit of *bryoniae* is at 700 m (Petersen 1955).

By their morphology the edge species are exposed to a different selection than the central species. The polyphagy of the central species leads to an increase of the variation of their populations. The greater variation of the central species by the combination of geographic variation and dispersal (Mayr 1954) is in this way increased.

		patterns			color			genitalia			larval foodplant	
		+	(+)	-	+	(+)	-	+	±?	-	Over- lapping	different
<u>Pieridae</u>	♂	4	5	0	6	1	3	2	1	7		
	♀	1	8	0	5	5	0				3(2)	5(6)
	total	5	13	0	11	6	3	2	1	7		
<u>Nymphalidae</u>	♂	2	4	1	2	1	4	5	2	0		
	♀	1	5	1	1	1	5				4	3
	total	3	9	2	3	2	9	5	2	0		

Table 2. Differences between sibling species of the families Meridae and Nymphalidae according to table 1.

ISOLATING MECHANISMS

Ethological isolation. The differences between species leading to ethological isolation are thus different in the two families investigated. Pieridae often have different colors and in at least two cases different scents (*G. hyale-australis* and *G. rhamnicleopatra*). Two species have separated from *P. napi* without developing recognizable scent differences.

The attractiveness of the color in *P. napi* is reduced to about 1/10 by a very small amount of yellow pterins in the wings (Peterson 1963 a p. 224). Bees in training experiments are able to separate four colors only (Hertz 1937). Perhaps the reaction of the *napi* butterflies means that a limit between two of the colors in their color vision is situated between white (without ultraviolet) and the same white with a slight mixture of yellow.

A similar slight difference is present in other pairs (*napi - ergane*, *rapae - manni*, and *cardamines - euphenoides*). It is possible that a + from the point of view of the butterflies is a better expression of the differences than the (+) of table 1.

The genitalia of many species of insects and other animals are often so characteristic that they enable the separation of closely related species (cf. Dobzhansky 1941 p. 267). This has given rise to the lock-key theory. According to this theory the genitalia of males and females of a species match another so exactly that even a small deviation makes copulation physiologically impossible. Some experiments and observations tend to support to the lock-key theory but others show that the original formulation was strongly exaggerated. Even after the removal of large parts of the genitalia except the aedeagus a male is able to copulate with a female of its own species (Sengün 1944, Lorkovic 1953). These results led to the conclusion that a structural change played no rôle in the isolation between species. No quantitative estimation of the isolation (e. g. by choice experiments) has ever been made. Observations by Standfuss (1896), Federley (1932), and Sturtevant (1921) show that different genitalia probably cause a certain isolation.

Differences between related species are more common where the genitalia have complicated structures as in the *Nymphalidae*. In groups with less complicated genital apparatus (as in fam. pieridae) inter- and intraspecific variation is smaller. Dobzhansky, (l. c.) suggests that a complicated structure is more often changed in connection with the genetic revolution within a population. However, this does not explain the evolution of the

complicated structures which in many groups are more common in the genitalia than in any other part of the body. This may be explained by a greater efficiency of a complicated genital apparatus. The possibility of a greater chance of developing isolation between species as a factor promoting complication of structure cannot be excluded. A character which permits rapid speciation (within reasonable limits) must in the long run have a positive selective value.

The ecological isolation is to a great extent dependent on the larval foodplant. The "typical" condition with a central species of wide distribution and a wide variety of foodplants and an edge species living on a single plant genus or species is present in only four (five) pairs (1, 3, 5, 10, perhaps also in 2), all of the family Pieridae. In another four pairs the foodplants are different, in seven (six) partly overlapping. No species have the same foodplants.

In four pairs one of the members is a lowland species, the other a mountain species. As a consequence of this difference not only a spatial but also a temporal isolation exists as the mountain species are on the wing later in the season.

Hybrids between sibling species have been found in several cases, though only within the family Pieridae. The hybrids between *C. eurytheme* and *philodice* show good though slightly lowered vitality (Hovanitz 1953). A similar result was obtained by Petersen and Tenow (1954) in crosses between sympatric *bryoniae* and *napi* from the northern Alps. In both cases the vitality of F₂-specimens was low. F₂-specimens of normal vitality were obtained by Bowden (1956) when crossing *P. bryoniae* from the Alps with English *napi*.

In the genus *Colias* a number of different hybrids have been found, for instance *sagartia* x *aurorina* (Lederer 1941) and *nastes* x *hecla* (Hovanitz 1963) among the pairs studied. Hovanitz (l. c.) mentions another seven combinations of *Colias* hybrids described in the literature.

In the genera *Pieris* and *Anthocaris* extensive hybridization experiments have been made by Lorkovic (1928, 1953). In crosses *P. manni* ♀ x *rapae* ♂ only males were obtained, a characteristic not uncommon among Lepidoptera. The reciprocal cross is in this respect normal. All hybrids are sterile. The ovaries of the females are rudimentary.

Hybrids were obtained in the following crosses too, though the sexes are not mentioned.

<i>P. napi</i> ♂	x	<i>ergane</i> ♀
<i>P. napi</i> ♂	x	<i>manni</i> ♀
<i>P. napi</i> ♂	x	<i>rapae</i> ♀
<i>A. cardamines</i> ♂	x	<i>euphenoides</i> ♀
<i>A. cardamines</i> ♂	x	<i>ausonia</i> ♀

Adult F_1 hybrids are thus obtained even between species less closely related than those counted as sibling species here. It seems, however, doubtful whether any of these hybrids exist in nature.

The fact that so many more hybrids of *Pieridae* than of *Nymphalidae* have been found in nature can be explained in several ways:

1. The *Pieridae* have in this respect been much more closely studied.

2. Hybrids are more easily detected in the *Pieridae* because of the clearcut difference in color and pattern.

3. Sibling species in the *Pieridae* are genetically more similar because genetically similar populations can become isolated ethologically by color differences.

Of the two families *Pieridae* and *Nymphalidae* the latter is the most successful in so far as it has a higher number of species. The only factor among those investigated which could be responsible for this is the more complicated structure of the genitalia. Only the investigation of a greater number of families could give the answer whether this is an important factor in the evolution of species.

SUMMARY

Ten pairs of sibling species, mainly European, of the family *Pieridae* and seven of the family *Nymphalidae* are compared. Differences in patterns, color, male genitalia, larval foodplants, and distribution have been investigated.

The *Pieridae* are more often different in color, the *Nymphalidae* in the male genitalia. The differences are of about the same size in the patterns of both families.

The differences in color between *Pierids* are attributed to the greater chance in this family of a mutation markedly changing the color due to the presence in the wings of chemically related pterins of white, yellow, and orange color. These colors are supposed to be sexual attractants and stimulants as has been proved for the white color of *P. napi*.

The greater differences in the genitalia between *Nymphalid*

species are connected with more complicated structures in this family.

The foodplants of the larvae are markedly different in 8 of the 15 pairs where they are known.

Species with a wide range usually live on a greater number of foodplants.

In almost all pairs one of the species lives in the Mediterranean area or is adapted to Arctic or alpine conditions. Only under such circumstances geographical isolation leading to speciation was possible.

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